

A REVIEW OF THE GENUS *TANGAROA* (ARANEAE, ULOBORIDAE)

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ABSTRACT

Characteristics of the genus *Tangaroa* are reviewed and the new species, *T. beattyi*, is described and compared with *T. dissimilis* (Berland) and *T. tahitiensis* (Berland). Cladistic analysis shows the first two species to be most closely related. The tetraspermathecate female genitalia of this genus show no evidence of fertilization ducts and appear to represent a transition state between haplogyne and entelegyne grades of organization.

INTRODUCTION

When Berland (1924) described the first *Tangaroa* species he remarked that it was aberrant and named it accordingly, *Uloborus dissimilis*. The unique characters he recognized were reduced anterior lateral eyes, the absence of abdominal tubercles characteristically found in uloborids, and the simple form of the male palpus. In mistaking mature females for subadults, he acknowledged a fourth character of the genus, the externally unmodified female genital region. The significance of these features was not formally recognized until Lehtinen (1967) established the genus *Tangaroa*. The genus was later restricted by removal of *U. waitakerensis* Chamberlain and further characterized as having haplogyne female genitalia and a presumptive male stridulatory apparatus consisting of an endite file and two setal picks on the cymbium (Opell 1979).

The purpose of this paper is to review the taxonomy of the genus and to present further evidence that female genitalia lack fertilization ducts and are, therefore, in the traditional sense, haplogyne. The former treatment is necessitated by discovery of a new *Tangaroa* species, and the latter is made possible by the availability of well preserved specimens of this species.

METHODS AND MATERIALS

Specimens of *Tangaroa beattyi* were fixed for about one month in Bouin's fixative, rinsed in several changes of 0.1 M sodium cacodylate buffer (pH 7.3), dehydrated through a graded series of acetone, and imbedded in Spurr's epoxy resin. Prior to examination, 1 μ m thick sections made with a Sorvall JB-4 microtome were stained with one percent toluidine blue in one percent borate buffer.

Scanning electron microscopy was performed on Bouin's-fixed specimens which were dehydrated in acetone, critical-point-dried, and vacuum evaporator coated first with carbon and then with gold-palladium.

Tangaroa Lehtinen

Tangaroa Lehtinen 1967:266, 391; Opell, 1979:474. Type species by original designation *Uloborus tahitiensis* Berland, 1934:323. The genus name is feminine.

Diagnosis.—Both males and females are distinguished from all other uloborids by having reduced anterior lateral eyes which are represented only by small pigment spots (Figs. 11, 18). Males are further characterized by the presence of a distal crook on the ventral surface of tibia I (Figs. 10, 14), a palpal femur whose length is at least three times that of the palpal trochanter (Fig. 2), and a folded or lobed distal cymbial region (Figs. 2, 9). Unlike males of other uloborid genera, those of *Tangaroa* lack an embolus guide and have a flattened embolus (Figs. 2, 9). Like *Waitkera* and *Polenecia* males, they have a presumptive stridulatory apparatus consisting of a file on the endite's lateral surface and distal cymbial picks (Figs. 1, 2). In *Tangaroa* there are two and in *Waitkera* three (Opell 1979, fig. 28) macrosetal picks. *Polenecia* males have two macrosetal picks plus an apical cymbial spine (Opell 1979, fig. 47).

Tangaroa contains the only uloborid females that lack external modifications of the genitalic area. Such modifications are slight, but discernable in *Waitkera* (Opell 1979, fig. 30). Openings are located on the posterior surface of the genital region, within the confines of the epigastric furrow. Each opening leads to two spermatheca, the ventral one bearing a slight swelling or lobe that appears to be a site of secretory activity (Figs. 6, 19, 21).

Tangaroa tahitiensis (Berland)

Figures 8-10, 18, 19; Table 1

Uloborus tahitiensis Berland 1934:323, 331, figs. 1, 6. Male holotype and three female paratypes in Muséum National d'Histoire Naturelle, Paris, examined.

Diagnosis.—This is the largest known *Tangaroa* species (Table 1). Males are distinguished by the first leg having seven macrosetae in or adjacent to the ventral tibial notch, four prolateral femoral macrosetae, and seven dorsal tibial macrosetae (Fig. 10). Females are characterized by having three prolateral macrosetae on femur I and by lacking dark pigment in the spiracular region.

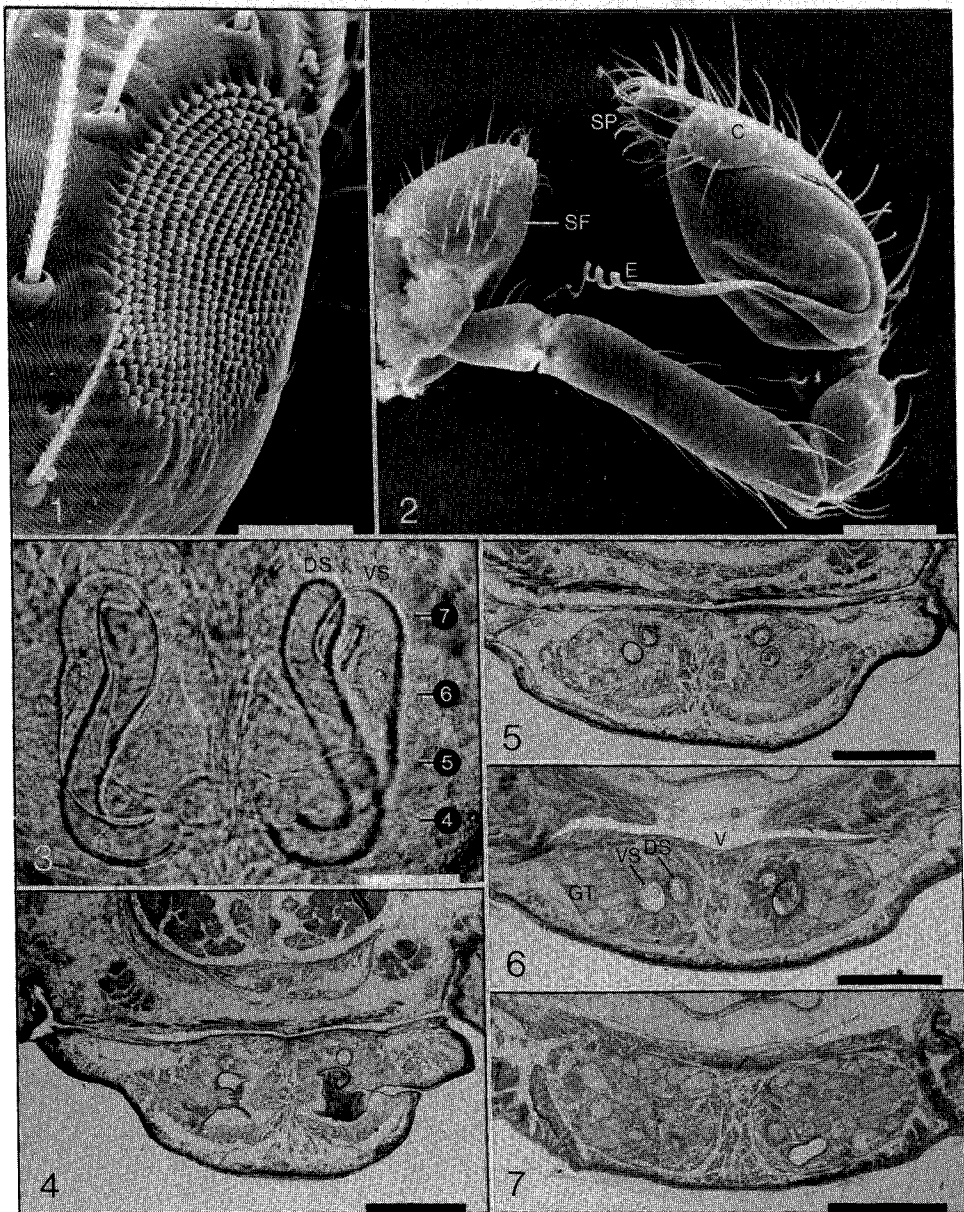
Distribution.—Tahiti, Society Islands; Rapa, Tubuai Islands.

Tangaroa dissimilis (Berland)

Figures 11-14, 20-22; Table 1

Uloborus dissimilis Berland 1924:176, figs. 18-20. Male paratype from Kone, female paratype from Mont Canala, New Caledonia.

Note.—Type specimens appear to have been lost. Illustrations and diagnosis are based on a male (AR 115) from Mt. Alempse (513 m.), Epi, New Hebrides, collected 21 Nov.

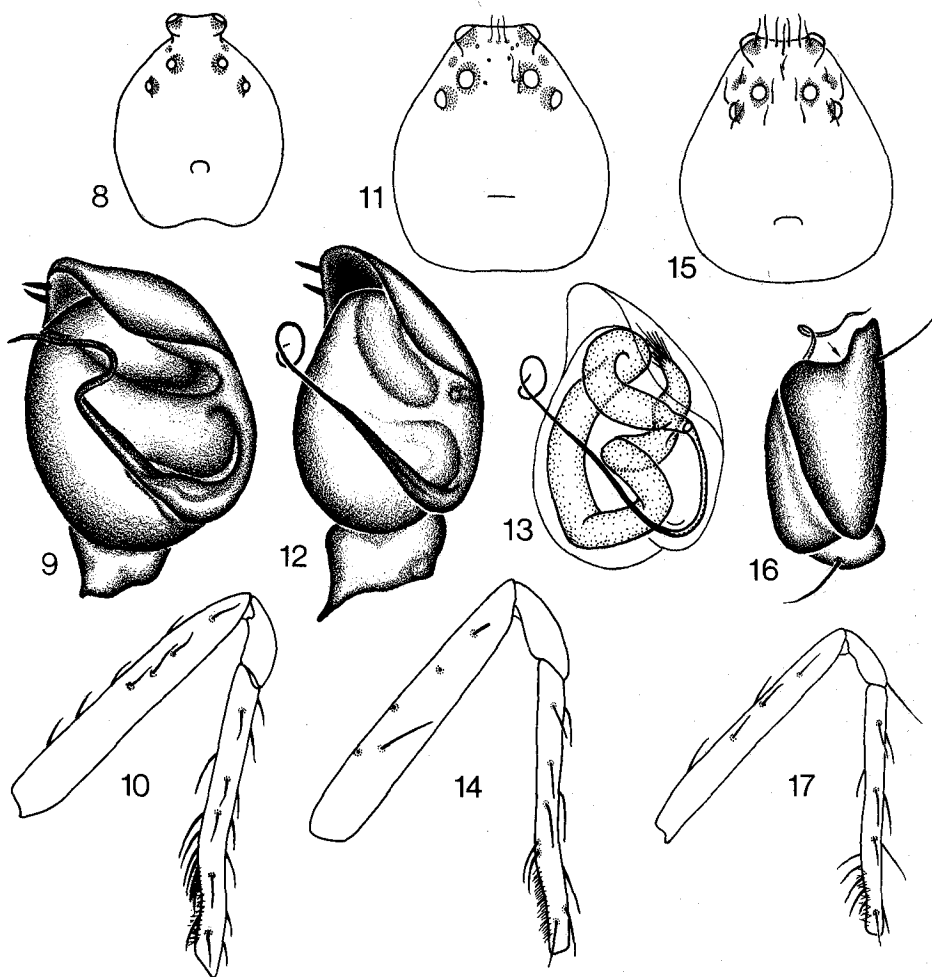


Figs. 1-7.—*Tangaroa beattyi*, new species: 1, Retrolateral view of male left endite showing stridulatory file; 2, Retrolateral view of male left palpus showing cymbium (C), embolus (E), and stridulatory picks (SP) and file (SF); 3, Dorsal view of cleared female genital region showing dorsal and ventral spermathecae (DS and VS, respectively); 4-7, Cross sections through female genital region (see Fig. 3 for position) showing spermathecae, glandular tissue (GT), and vagina (V). Scale line in Fig. 1, 20 μm . Fig. 2, 100 μm , and Figs. 3-7 50 μm .

1945 and deposited in the Muséum National d'Histoire Naturelle, and a female from Espiritu Santo, New Hebrides, collected May 1944 and deposited in the American Museum of Natural History.

Diagnosis.—This species is intermediate in size between *T. tahitiensis* and *T. beattyi* (Table 1). Males are distinguished by the first leg having two macrosetae adjacent to the distal tibial notch, two dorsal femoral macrosetae, and five dorsal tibial macrosetae (Fig. 14) and by having 11 ocular macrosetae (Fig. 11). Females are characterized by having three retrolateral macrosetae on the first femur, by having a pigmented spiracular area (Fig. 22), and by lacking genital macrosetae.

Distribution.—New Caledonia and New Hebrides.



Figs. 8-10.—*Tangaroa tahitiensis* (Berland): 8, Male carapace; 9, Retrolateral view of male left palpus; 10, Prolateral view of male left first femur, patella, and tibia.

Figs. 11-14.—*Tangaroa dissimilis* (Berland): 11, Male carapace; 12, Retrolateral view of male left palpus; 13, Retrolateral view of cleared male left palpus showing sperm ducts; 14, Prolateral view of male left first femur, patella, and tibia.

Figs. 15-17.—*Tangaroa beattyi*, new species: 15, Male carapace; 16, Median view of male palpus showing notched cymbium (arrow); 17, Prolateral view of male first femur, patella, and tibia.

Tangaroa beattyi, new species
Figures 1-7, 15-17, 23-24; Table 1

Types.—Male holotype and female paratype from nipa palms in swamp near Fanif, Yap Island, Caroline Islands, collected 14 April 1980 by Joseph Beatty. Male and female paratype from mouth of cave, Yap Island, collected 28 April 1980 by James Berry. Holotype and paratype in the Bishop Museum, others in the Museum of Comparative Zoology. This species is named for Joseph Beatty who along with James Berry collected it.

Diagnosis.—This is the smallest described *Tangaroa* species (Table 1). Males are distinguished by having three or four macrosetae in and adjacent to the ventral notch of tibia I (Fig. 17), by having 19 ocular macrosetae (Fig. 15), and by having a cymbial notch (Figs. 2, 16). Females are characterized by having an inverted, comma shaped pigment area around the PME's (Fig. 23), by having a pigmented spiracular region, and by having 15-17 genital macrosetae (Fig. 24).

Description.—Male. Total length 1.98 mm, carapace length 0.84 mm. When alive, members of both sexes were blue to light purple in color. Color patterns described here are those of alcohol preserved specimens. Carapace tan with gray posterolateral margins and gray circles around eyes (Fig. 15). Ocular region beset with about 19 stout setae (Fig. 15). Sternum tan with faint gray patches near coxae. Legs tan, the venter of each femur with a small, distal gray region. First leg macrosetae as presented in Table 1 and Fig. 17. Abdomen light tan with four faint, paraxial gray spots, a gray posterior tip, a ventrolateral gray stripe, and gray spiracular and epigastric regions. Male palpus (Figs. 2, 16) with a conspicuous retrolateral cymbial notch. The coiled embolus tip that appears in the palpi of both alcohol preserved and critical-point-dried specimens is probably an artifact of initial preservation. The embolus tip is least convoluted in *T. tahitiensis* (Fig. 9), indicating that distortion may increase as the embolus becomes thinner.

Female. Total length 2.06 mm, carapace length 0.76 mm. Carapace tan with posterolateral margins and gray circles around eyes, the PME's with an anterior gray extension (Fig. 23). Sternum tan with a posterior gray tip. Legs tan, each tibia with a faint gray distal ring. First leg setae as described in Table 1. Dorsum of abdomen light tan with posteriorly open V at its anterior margin, one or two pairs of central, paraxial gray spots, and a gray posterior tip. Lateral surface with a ventral gray stripe. Venter with light gray spiracular region and broad gray book lung patches (Fig. 24). Genital region slightly concave and beset with stout setae (Fig. 24). A pair of spermathecae extend from each of two posterior dorsal genital openings (Fig. 3). The dorsal spermathecae are more slender and expand only slightly, whereas the ventral pair expand near the center (at which point secretory tissue appears to surround them) and terminate in a narrowed loop (Figs. 3-7).

Natural History.—In both the field (J. Beatty and J. Berry, personal communication) and laboratory, *Tangaroa beattyi* immatures and mature females constructed small, horizontal orb-webs.

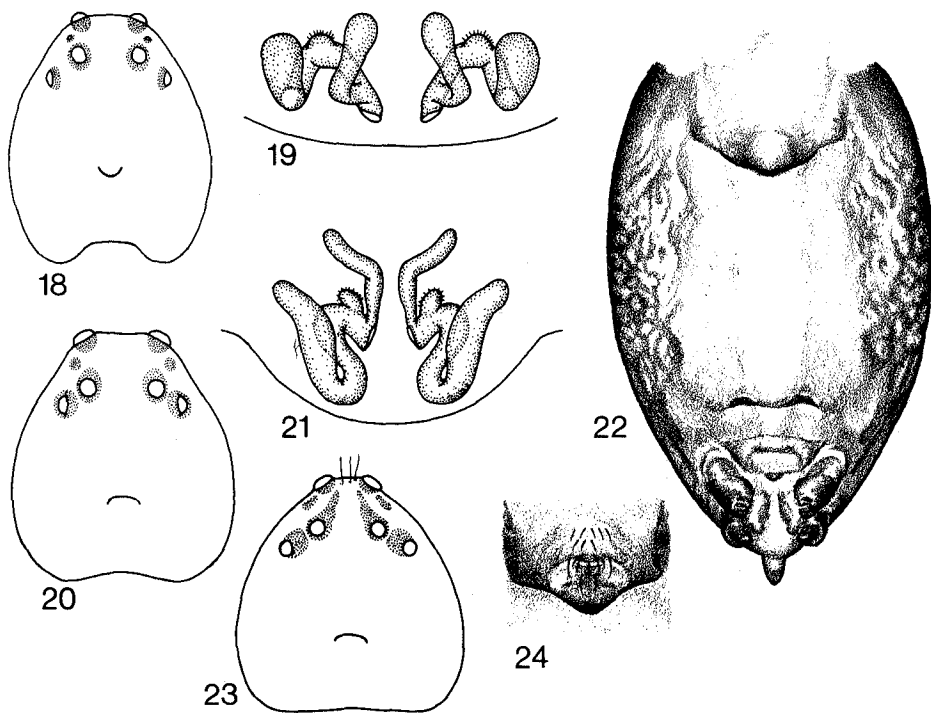
Distribution.—Known only from the type locality in the Caroline Islands.

DISCUSSION

Despite their geographical separation, a cladistic analysis shows *T. beattyi* and *T. dissimilis* to be more closely related to one another than either is to *T. tahitiensis* (Fig.

25). Because immatures have fewer setae than adults the lowest number of prolateral, dorsal, and retrolateral femoral and tibial macrosetae is considered to be the plesiomorphic state of these characters. The absence of ocular and genital macrosetae is, likewise, considered plesiomorphic. Of less certain polarity is the presence of a cymbial notch in males and spiracular area pigment in females. In both cases the absence of these features is considered plesiomorphic; although, a reversal of this polarity would change neither the cladogram nor the number of evolutionary steps required to explain it. A minimum of 18 evolutionary steps is required to explain distribution of the 12 2-state and three 3-state characters used in this analysis. The cladogram presented in Figure 25 requires a total of 18 character state changes.

The presumptive stridulatory apparatus of *Tangaroa* is found only in the family Uloboridae and here only in the three most primitive genera (Opell 1979). Its absence in other uloborids may indicate an increased reliance on web- rather than air-borne vibrations during courtship. Stridulatory devices have originated a number of times in spiders (Legendre 1963, Rovner 1975) and this particular device is probably an apomorphic character of early uloborids. The only alternate hypothesis is that the file represents the modified lateral region of a multiple row serrula similar to that found in *Hypochilus* (Platnick 1977, figs. 14, 15). The latter hypothesis is unlikely, as *Tangaroa*



Figs. 18-19.—*Tangaroa tahitiensis* (Berland): 18, Female carapace; 19, Dorsal view of cleared female genital region.

Figs. 20-22.—*Tangaroa dissimilis* (Berland): 20, Female carapace; 21, Dorsal view of cleared female genital region; 22, Ventral view of female abdomen.

Figs. 23-24.—*Tangaroa beattyi*, new species: 23, Female carapace; 24, Dorsal view of cleared female genital region.

females have only a single row serrula and males have a similar serrula along the endite's anterior margin. Additionally, it is ruled out by Platnick's (1977) conclusion that all non-hypochiloid Araneomorphae are derived from ancestors with simple serrulae. This conclusion was confirmed by examining eight (numbers 1, 2, 3, 4, 6, 9, 10, 12) of the twelve characters used by Platnick (1977, fig. 7) to evaluate the relationship of hypochiloids and other Araneomorphae. Of these, *Tangaroa* shares only the presence of tetraspermathecate female genitalia with the *Hypochilus* - *Ectatosticta* lineage.

The tetraspermathecate female genitalia of *Tangaroa*, like those of some other higher araneomorphs such as *Tetragnatha* (Levi 1981, Wiehle 1963) present a problem. Although their genitalia lack fertilization ducts and are similar to the primitive araneomorph pattern (Platnick and Gertsch 1976) found in *Hypochilus* (Kraus 1978, Gertsch 1958, 1964), Platnick (1977) has shown that all araneomorphs except *Hypochilus*, *Ectatosticta*, and *Hickmania* are derived from ancestors with a single pair of spermathecae. This suggests a fundamental difference between primary and secondary tetraspermathecate genitalia.

In bispermathecate spiders each spermatheca must store, nourish, and, when eggs are laid, probably activate quiescent spermatozoa (Kanwar 1967, Osaki 1969, Reger 1970, Sharma 1950, Sharma and Gupta 1956). In tetraspermathecate spiders derived from these ancestors, doubling of the spermathecae could be an adaptation either to increase volume for sperm storage or to partition storage and activation functions. Addition of proximally connected spermathecae in spiders which had already come to rely on a single pair seems a less efficient means of increasing storage volume than expanding the existing spermathecae. It would also introduce the problem of dividing the flow of semen from the male's embolus, which, judging from its length in *Tangaroa*, is probably inserted past the junction of the two spermathecae. As Kraus (1978) has noted, tetraspermathecate (2+2) neocribellates lack a wide, interconnecting vulval atrium that would permit the lateral flow of semen. In spiders which lack fertilization ducts this evidence favors origin of a second pair of proximally connected spermathecae to serve in sperm activation or another supplementary secretory function such as producing material which plugs the external genitalia of some spiders.

Small glands associated with the ventral spermathecae of *Tangaroa* (Figs. 19, 21) are similar to those borne on the lateral or terminal surfaces of *Hypochilus* and mygalomorph spermathecae (Brignoli 1980, Forster and Wilton 1968, Kraus 1978), indicating that the ventral pair is probably the primary pair.

Cross sections of *T. beattyi* female genitalia (Figs. 4-7) indicate that in the specimen examined only the right side was inseminated. On this side material is present in the lower (posterior) part of the ventral spermatheca (Fig. 4) and apparent secretory activity, as indicated by more darkly stained cytoplasm, surrounds the central region (Fig. 6) of both lateral spermathecae. Walls of the ventral spermathecae stain more darkly than those of the dorsal spermathecae.

Tangaroa appears to provide an example of a group intermediate between the haplogyne and truly entelegyne condition, a grade of organization similar to that referred to by Brignoli (1978) and Wiehle (1967) as the semientelegyne condition. The male's embolus can be inserted directly into a spermathecal duct, but, lacking fertilization ducts, female genitalia open into the confines of the epigastric furrow where exiting sperm are provided certain and protected contact with ova. Levi (1981) suggested that simple *Tetragnatha* female genitalia may be explained by cheliceral interlocking during courtship and the opportunity this affords for palpal alignment. Although courtship has not been reported

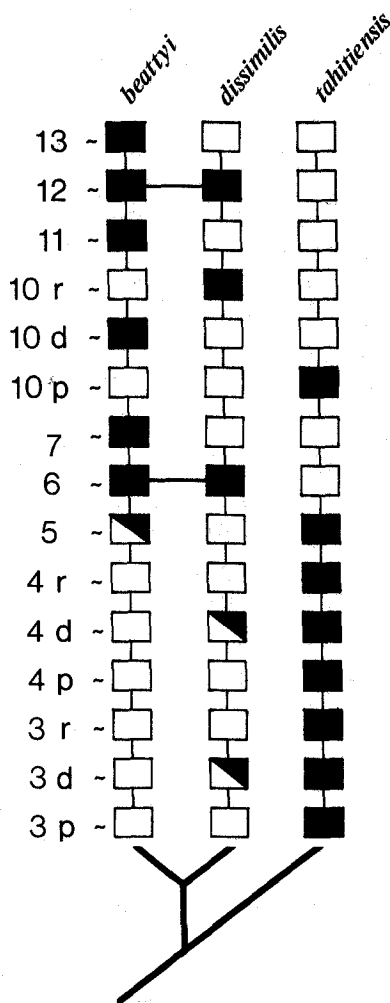


Fig. 25.—Cladogram of *Tangaroa* relationships. Numbers correspond to characters presented in Table 1, p, d, and r indicating prolateral, dorsal, and retrolateral macrosetae, respectively. White rectangles denote plesiomorphic character states and darkened and partially darkened rectangles apomorphic character states.

for *Tangaroa*, the first tibial crook unique to males of this genus may allow the male to firmly grasp the female and provide an analogous explanation for alignment of simple male and female genitalia.

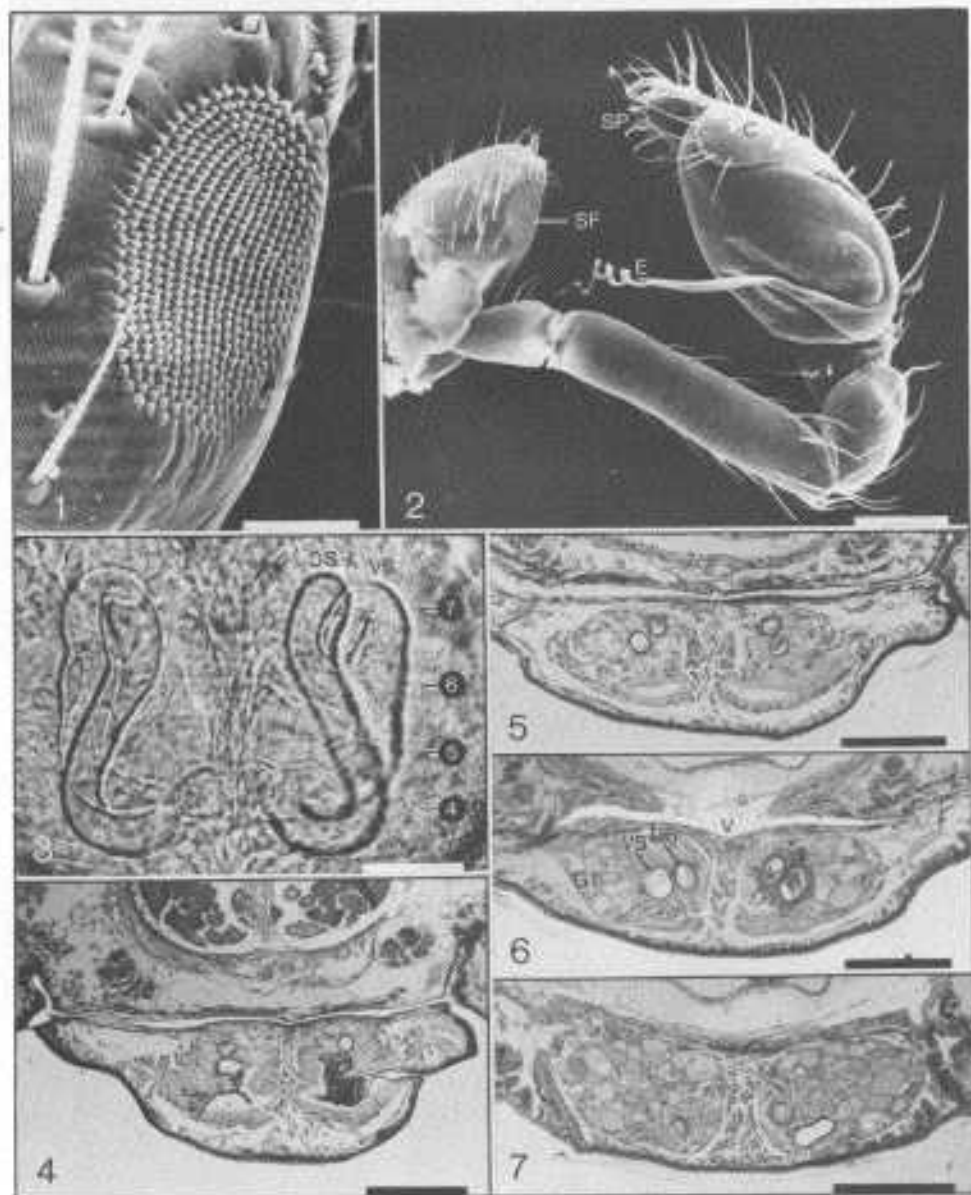
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LITERATURE CITED

- Berland, L. 1924. Araignées de la Nouvelle Calédonie et des îles Loyalty. In Sarszin and Roux, New Caledonia, Zoologie, 3(2):159-255.
- Berland, L. 1934. Araignées de Polynésie. Ann. Soc. ent. France, 103:321-336.
- Brignoli, P. M. 1978. Some remarks on the relationships between the haplogynae, the semientelegynae and the cribellatae (Araneae). Symp. Zool. Soc. London, No. 42:285-292.
- Brignoli, P. M. 1980. New morphological observations on some interesting genera of spiders (Araneae). Proc. 8th Intern. Arachnol. Cong., Vienna, pp. 371-376.
- Forster, R. R. and C. L. Wilton. 1968. The spiders of New Zealand, part II: Ctenizidae, Dipluridae, and Migidae. Otago Mus. Bull., 2:1-180.
- Gertsch, W. J. 1958. The spider family Hypochilidae. American Mus. Novitates, No. 1912:1-28.
- Gertsch, W. J. 1964. A review of the genus *Hypochilus* and a description of a new species from Colorado (Araneae, Hypochilidae). American Mus. Novitates, No. 2203:1-14.
- Kanwar, U. 1967. Histochemistry of spermatogenesis in the spider *Lycosa chaperi*. Res. Bull. (N. S.) Panjab Univ. (Sci.), 18:303-313.
- Kraus, O. 1978. *Liphistius* and the evolution of spider genitalia. Symp. Zool. Soc. London, No. 42:235-254.
- Legendre, R. 1963. L'audition et l'émission de sons chez les Aranéides. Ann. Biol., 2:371-390.
- Lehtinen, P. T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Ann. Zool., Fennici, 4:199-468.
- Levi, H. W. 1981. The American orb-weaving genera *Dolichognatha* and *Tetragnatha* north of Mexico (Araneae: Araneidae, Tetragnathinae). Bull. Mus. Comp. Zool., 149(5):271-318.
- Opell, B. D. 1979. Revision of the genera and tropical American species of the spider family Uloboridae. Bull. Mus. Comp. Zool., 148(10):443-549.
- Osaki, H. 1969. Electron microscope study on the spermatozoa of the liphistiid spider *Heptathele kimurai*. Acta Arachn., 22:1-14.
- Platnick, N. I. and W. J. Gertsch. 1976. The suborders of spiders: a cladistic analysis. American Mus. Novitates, No. 2607:1-15.
- Platnick, N. I. 1977. The hypochiloid spiders: a cladistic analysis with notes on the Atypoidea (Arachnida: Araneae). American Mus. Novitates, No. 2627:1-23.
- Reger, J. F. 1970. Spermatogenesis in the spider *Pisaurina* sp. a fine structure study. J. Morph., 130(4):421-433.
- Rovner, J. S. 1975. Sound production by Nearctic Spiders: a substratum-coupled stridulatory mechanism. Science, 190:1309-1310.
- Sharma, G. P. 1950. Spermatogenesis in the spider, *Plexippus paykulli*. Res. Bull. East Panjab Univ. (Zool.), 5:67-80.
- Sharma, G. P. and B. L. Gupta. 1956. Cytological studies on the male germ cells of the spider *Pardosa* sp., with observations under the phase contrast microscope. Res. Bull. Panjab Univ. (Zool.), 84:5-19.
- Wiehle, H. 1963. Spinnentiere order Arachnoidea (Araneae). XII. Tetragnathidae-Streckspinnen und Dickkiefer. Die Tierwelt Deutschlands. pt. 49, Jena, pp. 1-76.
- Wiehle, H. 1967. *Meta*—eine semientelegyne Gattung der Araneae. Senckenberg. Biol., 48:183-196.

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